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Factors Contributing to Interannual Variability in the Abundance of Bay Anchovy (Anchoa Mitchilli) Larvae

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by

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Dedication

To my fiancée Sarah. Thank you for your love and support.

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Abstract

Coastal ecosystems have been subject to increasing stressors over recent decades due to coastal development, human population growth, and climate change. Improving scientific understanding of the environmental factors which influence the productivity of fish populations in coastal ecosystems is vital to their prudent management, especially as the potential influence of anthropogenic climate change grows. Estuaries serve as critical habitats for many fishes of primary ecological, economic, and recreational importance. One such fish, the planktivorous Bay Anchovy (*Anchoa mitchilli*), is abundant along the Atlantic and Gulf coasts of the US and is a key prey resource for many estuarine and coastal piscivores. Within North Inlet-Winyah Bay estuary Georgetown, SC, the bay anchovy historically was one of the most abundant fishes in the system. However, recent surveys have suggested their populations have declined over the past 30 years. To determine what has contributed to the interannual variability in the fish's abundance, I used a suite of long-term data sets collected between 1981 and 2002 including biweekly collections of anchovy larvae, mesozooplankton including a calanoid copepod (*Acartia tonsa*), and chlorophyll-a (Chl-a) concentration as well as monthly river discharge. Here I explored how variability in the timing of life events (phenology) of *A. mitchilli*'s prey (as measured by copepod density) influenced interannual variability in larval abundance. I also tested how differences between *A. mitchilli* and copepod phenology could contribute to variability in *A. mitchilli* larval abundance. The influence of freshwater discharge on the interannual variability of *A. mitchilli* larval abundance was also explored.

I hypothesized that lower discharge rates could lead to decreased nutrient supply and therefore contribute to declines in Chl-a concentrations and copepod abundances, which would have negative influences on *A. mitchilli* larval abundance. Analysis revealed that river discharge and *A. mitchilli* larval density were inversely correlated, contradictory to what was hypothesized. Lack of significant relationship between copepods and *A. mitchilli* larval density may suggest that copepods are not a significant source of food for larval and adult bay anchovy within the system. Future work is required to fully assess the factors which contribute to the interannual variability in *A. mitchilli* larval density.

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Chapter 1

Interannual variability in phenology of a copepod species; implications in larval fish abundance

1.1 Introduction

Coastal ecosystems have been subject to increasing stressors over the past several decades due to coastal development, human population growth, and climate change (Kennish, 2002; Paerl et al., 2006). Improving scientific understanding of the environmental factors which influence the productivity of fish populations in coastal ecosystems is vital to their prudent management and utilization, especially as the potential impacts of anthropogenic climate change grows in the future. Estuaries act as critical habitat for many fish of primary ecological, economic, and recreational importance (Boehlert and Mundy, 1986). Use of these habitats by fish during their larval stages is well documented (Boehlert and Mundy, 1986; Allen and Barker, 1990; Beck et al. 2001). However, understanding the factors that influence interannual variability in the recruitment of coastal fishes continues to elude scientists as it has over the past century (Hjort, 1914). Cushing (1975) proposed a hypothesis to address this variability, suggesting that interannual variation in the survival and eventual recruitment of larval fishes could be explained by the degree to which the timing of plankton production coincides with larval fish production. Thus, Cushing's match-mismatch hypothesis proposes that year class strength is dependent on phenological variability (i.e., the timing of life events) between trophic levels. More recently, the hypothesis has been extended

to piscivorous fish species and their associated prey (Durant et al., 2013), to subtropical regions (Cushing, 1990), and to investigate how climate change may affect trophic dynamics (Durant et al., 2007). A common response of phenology to climate variability is shifts in the seasonal timing of arrival or maximum abundance (Edwards and Richardson, 2004, Thackeray, 2012). Additional research has revealed the importance of high levels of prey in promoting high survival rates during the larval fish period (Cushing, 1990, 1995; Lasker, 1985; Rilling and Houde, 1999) considering low prey levels could lead to slow larval growth, introduce poor nutritional condition, and increase predation risk (Houde, 2008). Phenological shifts in the prey of the larvae could therefore result in de-synchronization between larval stages of the predator and their associated prey and this mismatch could result in reduced recruitment (Thackeray, 2012).

Larvae of members from Sciaenidae, Clupeidae, and Engraulidae families can be found throughout intertidal creeks of North Inlet Estuary, Georgetown, SC (Allen and Barker, 1990). One species of the Engraulidae family, the Bay Anchovy (*Anchoa mitchilli*) is particularly abundant and represents a critical trophic link in estuarine food webs (Jonhson et al., 1990; Scharf et al., 2002). The fish has a large geographic range within the Western Atlantic and Gulf of Mexico. It is short lived (<2 years) and highly iteroparous with >90% of the egg production within a season coming from age-1 females (Peebles et al., 1996). Within North Inlet estuary, SC (USA), adults primarily feed on crab megalopae, crab zoea, veliger larvae, and calanoid copepod species (adults and copepodids) (Johnson et al., 1990). Populations of *A. mitchilli* are also highly abundant in other systems including Chesapeake Bay (Rilling and Houde, 1999) and Tampa Bay (Peebles et al., 1996).

Ogburn et al. (1988) conducted a 4-year study which revealed *A. mitchilli* to be the most abundant fish species in spring and summer within North Inlet. Although historically abundant in North Inlet (Allen and Barker, 1990), scientific surveys have suggested their populations have declined over the past 30 years. Similar declines of this species have been noted in additional systems including Chesapeake Bay (Kimmel et al., 2012). Kimmel et al. (2012) proposed that the fish's long-term decline was due to reduction in their prey, *Acartia tonsa* ultimately in response to increased eutrophication, hypoxia occurrence, and predator abundance. The importance of *A. tonsa* in the diet of adult and larval bay anchovy has been well studied (Detwyler and Houde, 1970; Johnson et al., 1990; Peebles et al. 1996). Peebles et al. (1996) suggests adult *A. mitchilli* that are income spawners (i.e., their fecundity is reliant on prey levels at and shortly before spawning) and that *A. tonsa* was their primary prey in the Tampa Bay system. The seasonality of *A. mitchilli* is relatively fixed, typically occurring between April and September in Winyah Bay (Allen et al. 2008), and coincides with that of *A. tonsa* in southeastern estuaries (Sullivan et al., 2007). Yet, the extent to which food availability, specifically the timing of food availability relative to the period of peak larval production, could influence the interannual variability in recruitment of the bay anchovy has yet to be studied.

Improved understanding of how changes in the timing of seasonal events influences the survival of *A. mitchilli* may offer insight to the sensitivity of the coastal ecosystems to phenological shifts associated with climate variability. Here I use a suite of long-term data sets to explore if changes in the timing of production, as measured by abundance, of a calanoid species, *A. tonsa*, is correlated with variability in the abundance

of the bay anchovy on interannual timescales. Biweekly collections of *A. tonsa* from 1981-2003 allowed us to characterize dates of maximum abundance in each year and compare those dates to annual larval bay anchovy densities. I hypothesized that large differences between dates of maximum occurrence of copepodids and adults and arrival dates of anchovy larvae could contribute to declines in larval anchovy abundance.

1.2 Methods

1.2.1 Study Area

The North Inlet-Winyah Bay NERR is located within Georgetown County along the coast of South Carolina. The Winyah Bay (WB) watershed is the third largest watershed along the east coast of the US; only Chesapeake Bay, VA and Pamlico-Albermarle, NC systems are larger. The watershed is approximately 46619 km^2 and extends across portions of Virginia, North Carolina, and South Carolina (Buzzelli et al., 2004). Nearly 25% of South Carolina's and nearly 20% of North Carolina's total land area are included within the watershed. The main source of freshwater input into the system is received through the Pee Dee-Yadkin river system (>85%) (Patchineelum et al., 1999). The estuary itself is approximately 65-km^2 with a mean depth of about 4.2-m. Adjacent land usage can be characterized as industrial, agricultural, forested, natural, and managed wetland (Buzzelli et al., 2004).

The North Inlet (NI) (33°20' N, 79°10' W) watershed is much smaller than WB; only comprising approximately 38-km^2. However, its surrounding areas are much less developed; only about 2% are developed. It is connected to WB by a shallow basin known as Mud Bay. Through this connection, WB acts as a source of freshwater input to NI as do some small streams and groundwater seepage. The estuary is a *Spartina*

alterniflora dominated salt marsh with a tidal range of approximately 1.5-m. It is a well-mixed system with salinities typically ranging from 30-35.

Biological time series data were collected at two sites within NI. Zooplankton collections were made at one site at the long term sampling site BB; a subtidal channel which has an depths range between 2.5 and 4 m at low tide (Allen and Barker, 1990). BB is located at the confluence of two creeks, Town and Clambank (CB) (**Fig. 1.1**). It is positioned approximately 2-km from the mouth of NI and 3 km from WB. The bottom can be described as muddy with growths of soft coral and sponges. The site is located about 3.5-km west of the mouth of NI. It can be characterized as a narrow tidal creek surrounded by oyster reefs and *S. alterniflora* (Buzzelli et al. 2004).

1.2.2 Biological Sampling

Ichthyoplankton and mesozooplankton collections were made every 10-16 days between 1000 and 1600 hours approximately 1.5 hours before the predicted low tide beginning in January of 1981. Ichthyoplankton samples were collected with an epibenthic sled consisting of a rectangular steel frame (51 x 30 cm), fitted with a 365-μm-mesh net. Skis were mounted to the frame so that the apparatus could be towed along the bottom. The sled was fitted with a General Oceanics flowmeter to estimate water volume filtered. Tows were made from a small boat and were made in the same direction of the ebbing tidal current. Three sequential tows were made along 100-m paths which are marked by stakes at site BB. Collections were preserved in formalin and stained with rose bengal (0.5 g L^{-1}). Physical data including bottom and surface temperature and salinity were measured simultaneously using a YSI. In the laboratory, typically entire samples were analyzed and the total number of larval fish was counted.

In some cases, a Folsom splitter was used to produce a subsample no less than 12.5% of the original sample. Larvae were first identified to the genus level and therefore both *Anchoa mitchilli* and *Anchoa hepsetus* were included in counts and labeled as *Anchoa spp.* More recently, larvae have been identified to species level which has allowed us to characterize the taxonomic composition. Of the 434 individual samples in which larval *Anchoa spp*. were identified between 1981 and 2013, 283 contained *A. mitchilli* while *A. hepsetus* were only present in three. Thus, for our analysis I assume that all larvae captured are *A. mitchilli*. For each tow larval densities were calculated by dividing total number of larvae by the total volume of water filtered. Larval densities for an individual date represent an average of the three replicates. Larval fish data were available for the years of 1981-2013. However, for our analysis I only consider data collected between 1981 and 2002 due to the availability of mesozooplankton data.

Mesozooplankton samples were collected using 0.5-m ring nets fitted with a 153-μm-mesh net and a General Oceanics flowmeter. Weights were attached to nets so that they would reach the bottom of the water column. A release mechanism was installed on each net so that it remained closed until it reached the bottom. Two simultaneous tows were completed at site BB. Nets were towed with the current and remained on the bottom for 5 minutes after which they were raised to just below the surface for an additional 5 minutes. Collections were preserved in formalin and stained with rose bengal (0.5 g L^{-1}). For laboratory processing, each sample was filtered through a 153-μm sieve, and the total sample volume was brought up to 100 mL or 200 mL depending on sample density. A 2-mL Stempel pipette was used to take a subsample, and the total number of *A. tonsa* adults and copepodids and total number of all copepods

were counted. The total number was multiplied by a multiplication factor determined by the total sample volume (e.g., 50x if the sample volume was 100-mL). Densities were calculated for each replicate by dividing total counts corrected with dilution factor by the total volume of water filtered. Densities for an individual date represent an average of the two replicates. Mesozooplankton data were processed for the years of 1981-1991, 1996-1998, and 2001-2002.

1.2.3 Data Analysis

The densities (number m^{-3}) of *Acartia tonsa* adults and copepodids and *Anchoa mitchilli* larvae were calculated for each sample. Raw densities were log transformed to normalize the distribution prior to averaging. These logged abundance values were used to calculate monthly and yearly averages. Date of first occurrence within a given year for bay anchovy larvae represent the date of sampling in which their abundance exceeded 0 for two consecutive sampling dates. Date of first occurrence within a given year for adults and copepodids was determined by using a threshold of 1000 individuals m^{-3}. Houde, (1978) showed that nauplii densities of 100,000 individuals m^{-3} promoted survival through metamorphosis of 10% of *A. mitchilli* larvae in incubation experiments. Based on defined a ratio of nauplii to adult *A. tonsa* (100:1) within the Patuxent River estuary, this equates to 1,000 individuals m^{-3} (Heinle, 1966). When densities exceeded the threshold for two consecutive sampling dates, the corresponding date to first exceed 1000 individuals m^{-3} were recorded as the date of first occurrence. For years when densities did not exceed the established threshold, the date of maximum abundance was used as the date of first appearance. The date of maximum abundance for A. tonsa adults and copepodids and larval anchovy was determined for each sampling

year for which data was available. The values represent the Julian date that the yearly maximum value was collected. Significant relationships were tested using Pearson's correlation test with a confidence interval set at 95%. Long-term trends were tested for significance using linear regression analysis.

1.3 Results

1.3.1 Long-term Trends

A significant negative trend ($p<0.01$) was noted in yearly average densities of *A. tonsa* adults and copepodids and monthly average densities of *A. mitchilli* larvae from 1981-2002. *A. tonsa* adult's maximum density was recorded on 06/29/1981 (~24561 individuals m^{-3}) and copepodids maximum density was recorded on the same date and measured approximately 48,616 individuals m^{-3}. The overall average density of adults and copepodids was approximately 1317 and 3670 individuals m^{-3} respectively. The maximum number of *Anchoa* larvae was recoded 4/30/1981 (~10 individuals m^{-3}) (**Fig. 1.2**).

1.3.2 Phenological Dates

No long-term trends in date of maximum occurrence were noted for *A. tonsa* adults and copepodids between 1981 and 2002 (**Fig. 1.3A**). The average date of maximum occurrence for *A. tonsa* adults and copepodids was the 172nd day (June 21) and 181st day (June 30) respectively. The latest date of maximum occurrence for both *A. tonsa* adults and copepodids was 09/11/1985. The earliest date of maximum occurrence for adults and copepodids was 05/06/1986 and 04/29/1988 respectively. A close to significant increase in date of maximum occurrence was noted for *A. mitchilli* ($r=0.398$, $p=0.067$). Their average date of maximum abundance was the 163rd day (June 12). The

latest date of maximum occurrence was recorded on 07/11/1996, and the earliest was recorded on 04/24/2002.

No long-term trends in date of first occurrence were noted for *A. tonsa* adults abundances (**Fig. 1.3B**). A significant increase in date of first occurrence was recorded for *A. tonsa* copepodids ($r=0.56$, $p<0.05$). Average date of first occurrence for *A. tonsa* adults and copepodids was the 144 (May 24) and 120 (April 30) respectively. A significant increase in date of first occurrence was recorded for *A. mitchilli* ($r=0.504$, $p<0.05$). Average arrival day for anchovy larvae was the 113^{th} day (April 23). The earliest day of first occurrence was recorded on 04/3/1985 and the latest on 06/09/1983.

1.3.3 Phenological Dates and Interannual Variability in Abundance

The date of maximum occurrence for *A. tonsa* adults and copepodids was compared to yearly averages of *A. mitchilli*, and no significant relationship was detected during the 1981 and 2003 period (**Fig. 1.4**). The difference between date of first occurrence anchovy larvae and date of maximum occurrence for *A. tonsa* adults and copepodids was calculated. No significant correlation between the difference in phenological dates and yearly anchovy densities was found (**Fig. 1.5**). Similar, non-significant results were present when comparing differences in date of maximum occurrence for each group and yearly averages of larval density (**Fig. 1.6**). When compared to yearly larval densities, comparisons of the difference in date of maximum occurrence of *A. mitchilli* larvae and arrival date of copepodids and adults did not exhibit a significant relationship (**Fig. 1.7**). Comparisons of differences in arrival dates for each group also displayed no significant relationship to larval average density (**Fig. 1.8**).

1.4 Discussion

Cushing (1975) proposed a hypothesis which aimed to address why there was such large interannual variability in larval fish recruitment. He argued that year class strength is reliant on the degree to which larval first feeding coincides with peak plankton production. More recently, marine plankton production cycles have been widely reported to be shifting in response to climate change (Root et al., 2003; Thackeray et al., 2012). As a result, there has been concern for de-synchronization between key seasonal species interactions (George, 2012; Thackeray et al., 2012). In most coastal estuaries, copepods dominate the mesozooplankton and act as a critical link between phytoplankton and upper trophic levels, specifically larval fish (Ji et al., 2010).

Within NI-WB one of those species of copepod, *A. tonsa*, is highly abundant and is documented to be a component of adult bay anchovy prey (Johnson et al. 1990). Using multiple long-term data sets, it was my goal to explore if there was a match/mismatch dynamic operating between bay anchovy and *A. tonsa* within North Inlet. The dates of first appearance and maximum abundance were determined for each species between 1981 and 2002. I hypothesized that phenological differences between the two groups may contribute to reduced larval fish production and therefore be related to the interannual variability in larval abundance. Drawing quantitative conclusions relating changes in phenology of marine species directly to abundance of higher trophic species has proven to be difficult (Ji et al., 2010). This fact is reflected in our own results. No significant, linear relationship between phenology differences of *A. tonsa* and *A. mitchilli* abundances were present.

It was also our goal to explore phenological shifts in relation to the interannual variability noted in *A. mitchilli* densities between 1981 and 2002. Despite a temporal sampling strategy adequate to resolve phenological variability (biweekly, as defined by Edwards and Richardson, 2004; Ji et al., 2010), my analysis only revealed a long-term trend increase in *A. tonsa* copepodid arrival and *A. mitchilli* date of maximum abundance. I express phenological dates as days of the year and although Edwards and Richardson (2004) established that biweekly samples are adequate to describe phenology of marine organisms, I suggest that weekly values will allow for a more precise analysis especially when comparing across trophic levels. Although trends in anchovy phenology were found, no relationship with *A. tonsa* was established. Lack of a relationship between zooplankton phenology, larval anchovy phenology, and larval abundance may indicate that there is an alternative mechanism which could be contributing to the interannual variability in larval fish abundances. It may also be possible that the measure used for phenology within this study may not have been optimal. I characterized the date of arrival and maximum abundance for both species. Multiple alternative phenological dates could have been used, see Ji et al. (2010) for review. Additionally, the threshold used to determine date of first occurrence for *A. tonsa* adults and copepodids (1000 individuals m^{-3}) could have affected our calculation of the date of first appearance. Alternative thresholds could have been used and may have yielded alternative results. Ultimately, this analysis would have benefited from a combination of more temporal inclusive data and alternative thresholds.

Due to the limitations of using available data, I used larval abundance to attempt to draw conclusions about the stock as a whole. The logic stemmed from the

established relationship between *A. tonsa* abundance and egg production by female anchovy within Tampa Bay (Peebles et al., 1996). From this I assumed that more copepods were indicative of more eggs and therefore more larvae. If long-term datasets of adult stock or recruitment (e.g., juvenile abundance index) were available within this system, my hypothesis may not have been rejected. I am also assuming that *A. tonsa* is the primary food source for both adult and larvae *A. mitchilli*. Johnson et al. (1990) conducted a study to characterize prey selection by adult bay anchovy relative to prey availability within NI. They found that although *A. tonsa* comprised nearly 47% of the total zooplankton collected, they only accounted for approximately 7% of the adult diet. In this study, *A. tonsa* comprised only 35% of total copepod density on average. Thus, this study would have benefited from knowledge of what adults are consuming while spawning and what larvae are eating after fully consuming their yolk sac.

Factors contributing to interannual the variability in larval fish recruitment have been the focus of many studies over the past century (Hjort, 1914; Cushing, 1975; Lasker, 1985; Boehlert and Mundy, 1988). Here it was my goal to contribute to the knowledge of recruitment dynamics of an ecologically significant planktivorous species, the bay anchovy. Although, no significant evidence was discovered supporting Cushing's (1975) match/mismatch hypothesis within this system, some conclusions can be drawn. Coastal estuaries are highly diverse systems and the processes which act on the organisms which reside there are not only numerous but also complex (Wetz et al., 2011). Thus, there is most likely an alternative mechanism influencing the interannual variability in larval abundance and contributing to this long-term decline. Additionally, although the phenological timing of *A. tonsa* production seems to not be related to larval

abundance, it is possible that the magnitude of its densities could be. In Chapter 2 I explore the extent to which the interannual variability in copepod abundance could influence the interannual variability in larval *A. mitchilli* abundance.

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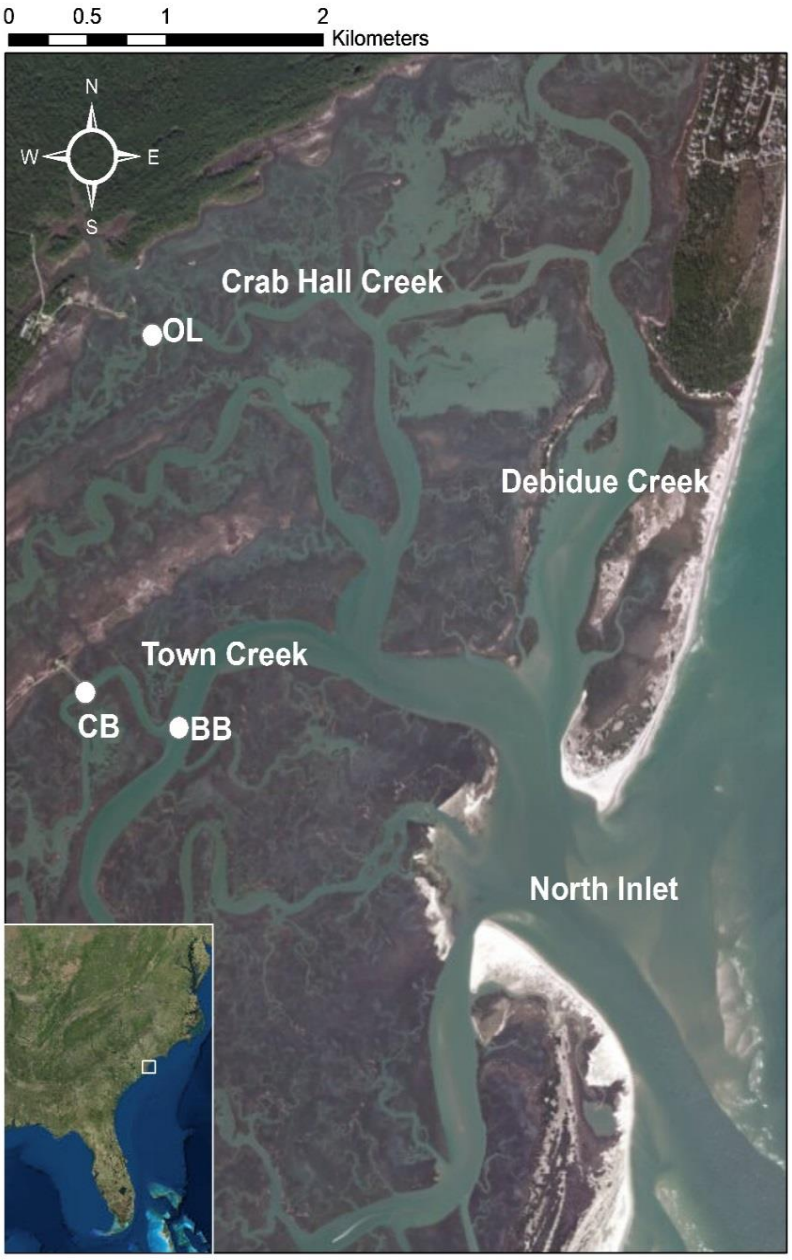

Figure 1.1 Map of North Inlet Georgetown, SC. Stations of long-term sampling (OL, CB, and BB) are designated by white markers. Major creeks are also indicated.

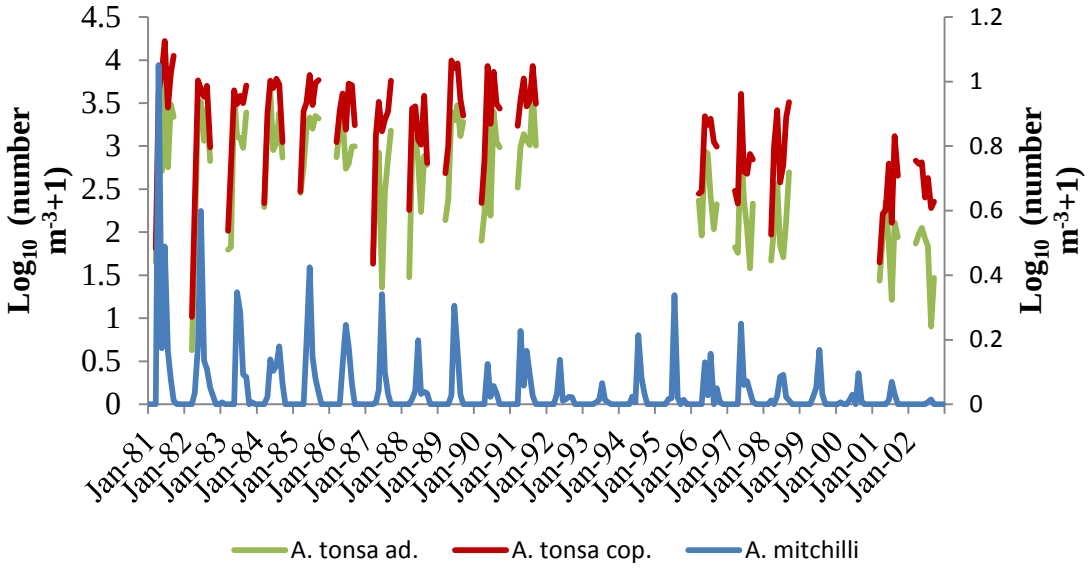

Figure 1.2 Time series of monthly average *A. tonsa* adults (ad.) and copepodids (cop.) (primary y-axis) and *Anchoa mitchilli*. larval densities (secondary y-axis) between 1981 and 2002.

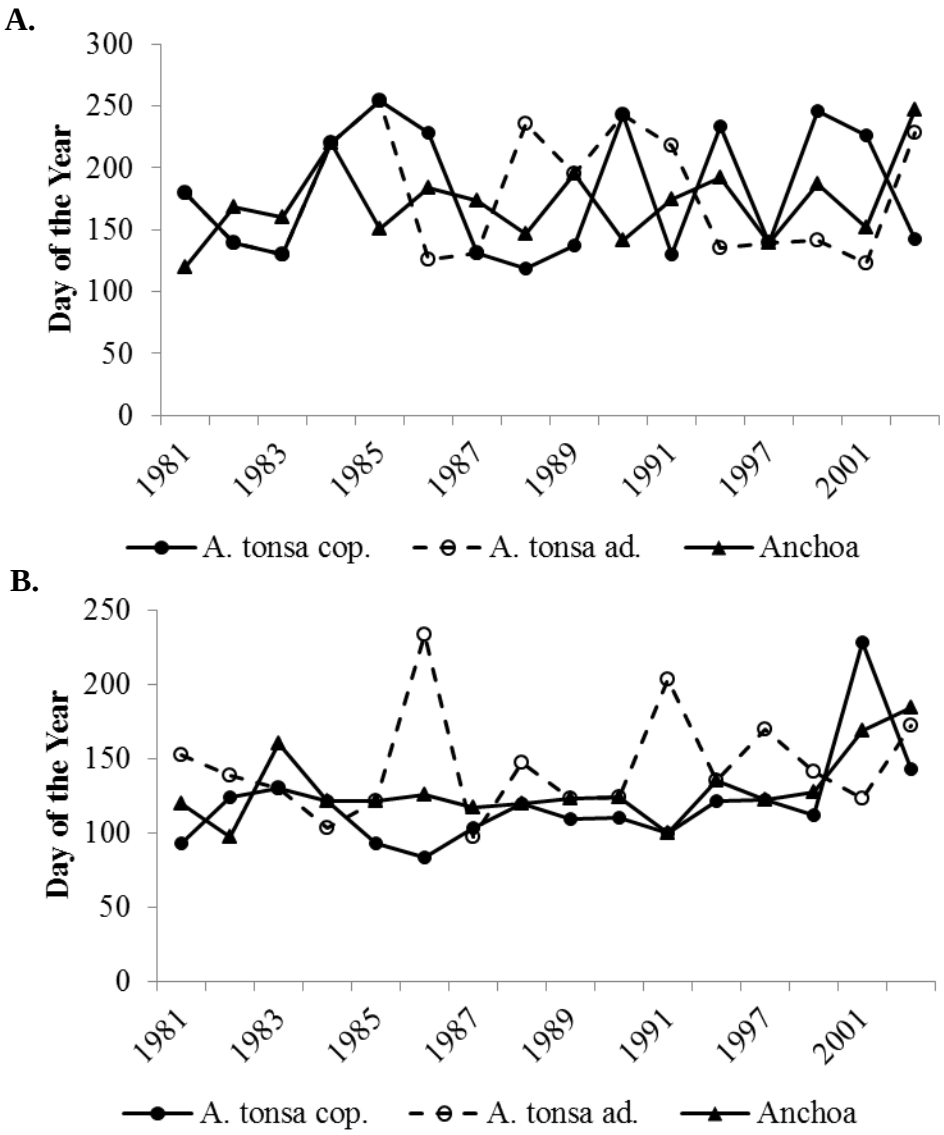

Figure 1.3 Dates of maximum abundance (**A**) and arrival (**B**) for *Acartia tonsa* adults and copepodids and for *Anchoa mitchilli* densities.

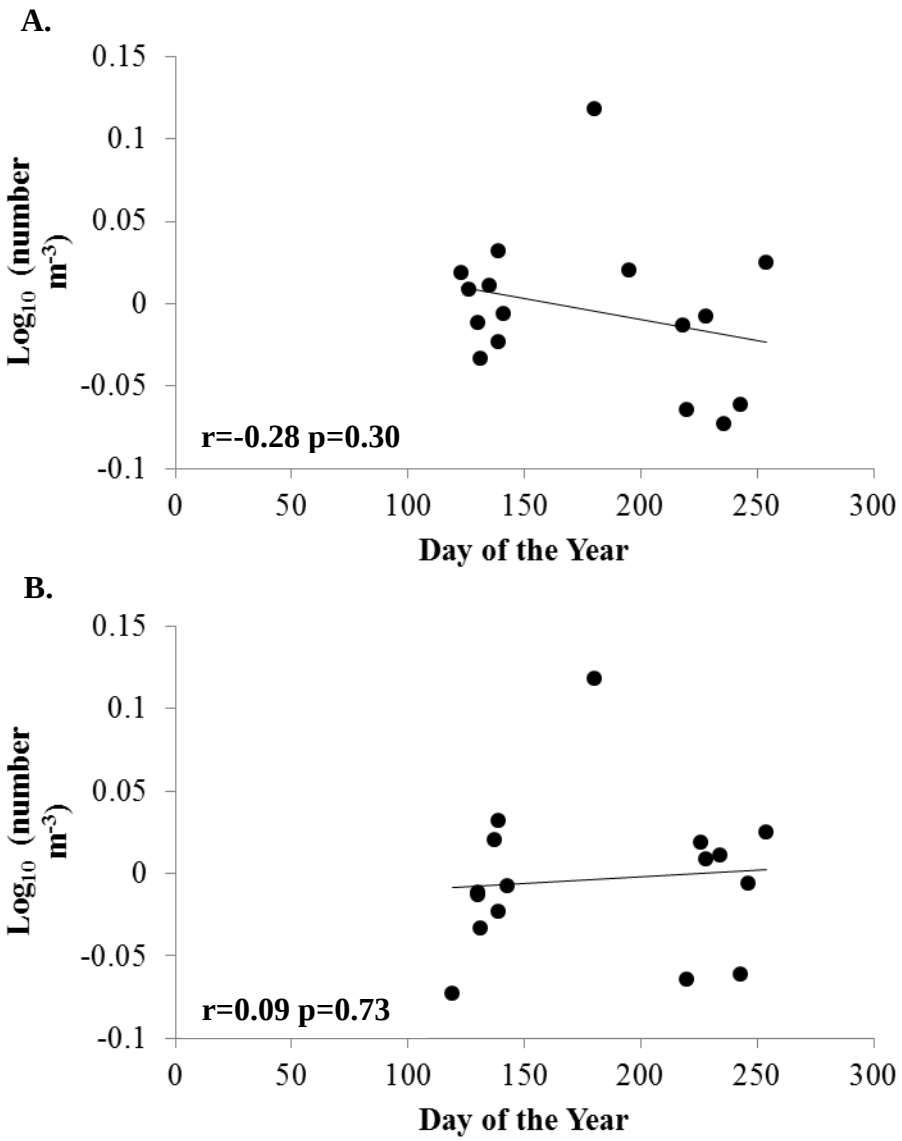

Figure 1.4 Date of maximum occurrence for *A. tonsa* adults (**A**) and copepodids (**B**) and detrended yearly average *Anchoa mitchilli* densities for data between March and September.

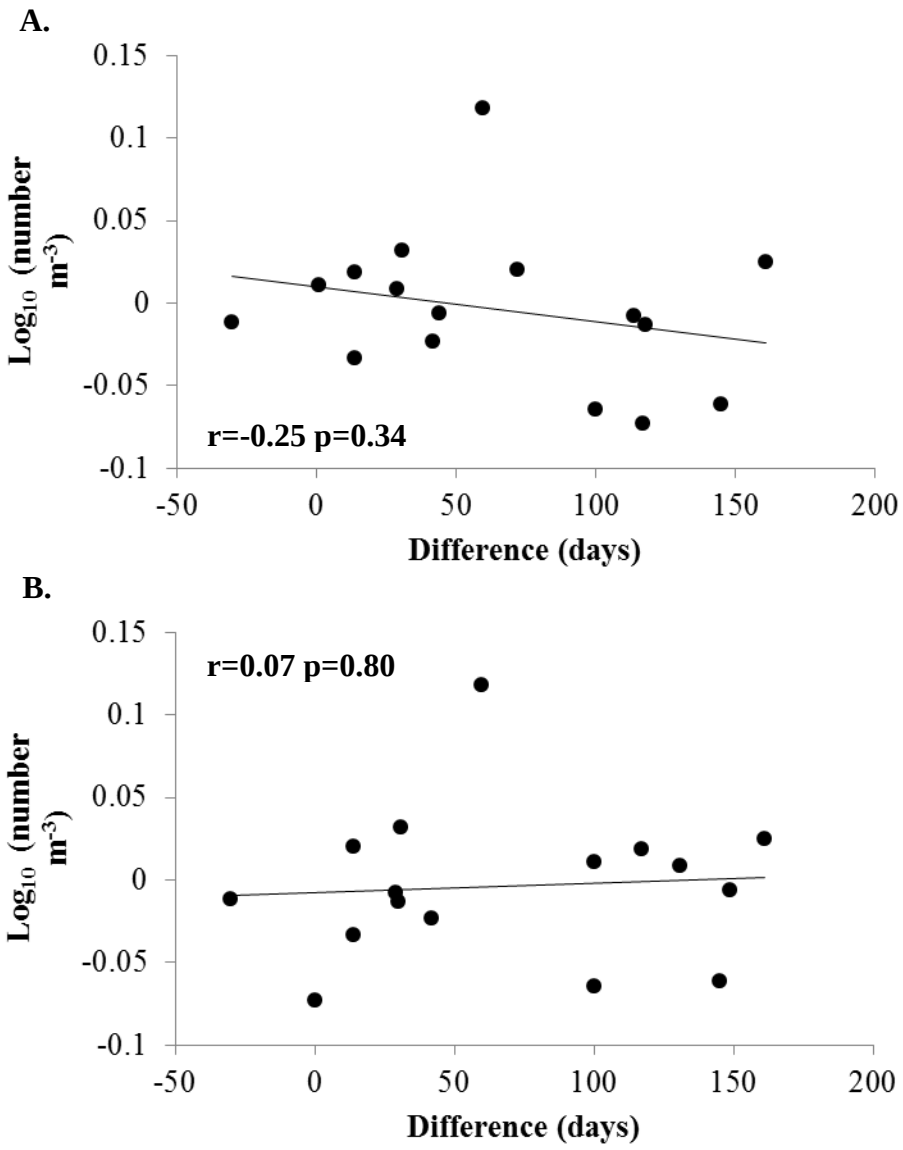

Figure 1.5 Difference in date of first appearance of *Anchoa mitchilli* and date of maximum occurrence *A. tonsa* adults (A) and copepodids (B) against detrended yearly average *A. mitchilli* densities.

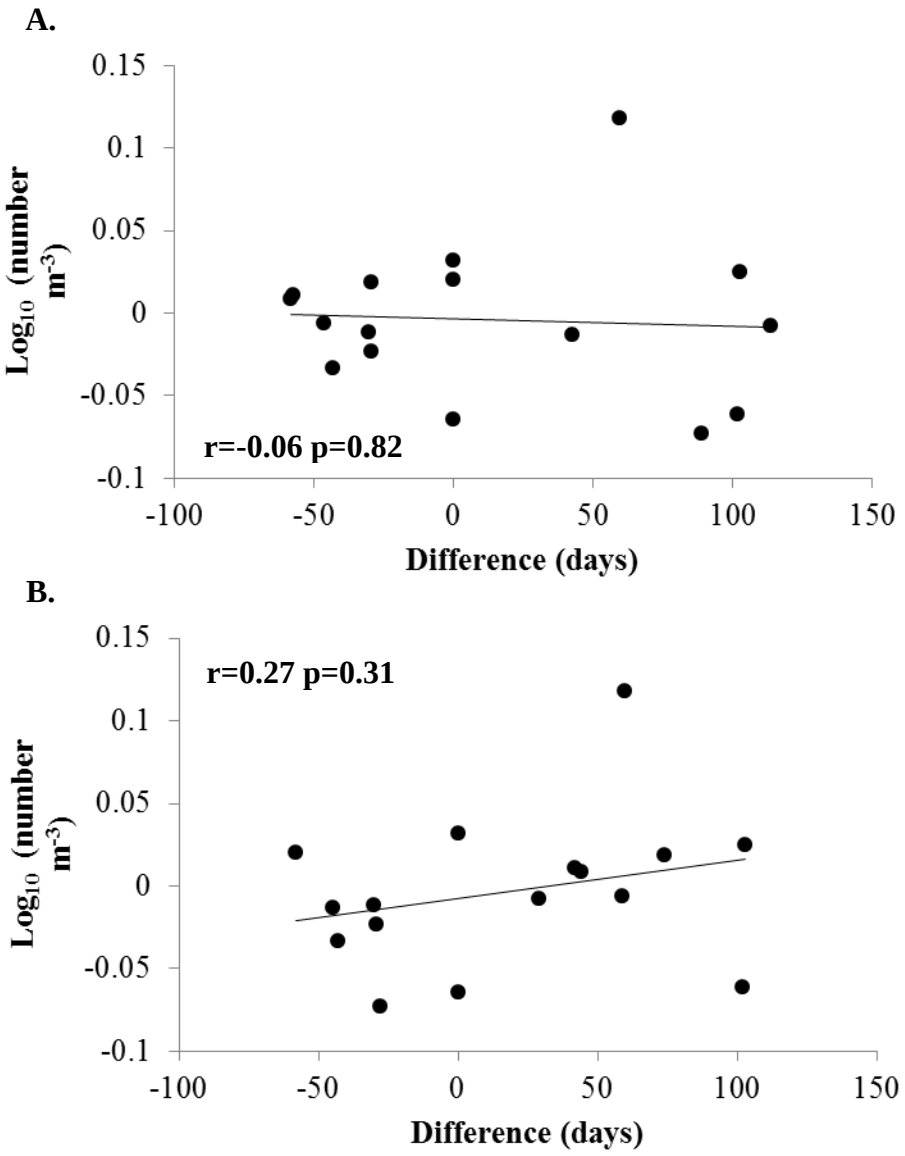

Figure 1.6 Difference in date of maximum occurrence of *Anchoa mitchilli* and *A. tonsa* adults (A) and copepodids (B) against detrended yearly average *A. mitchilli* densities for data between March and September.

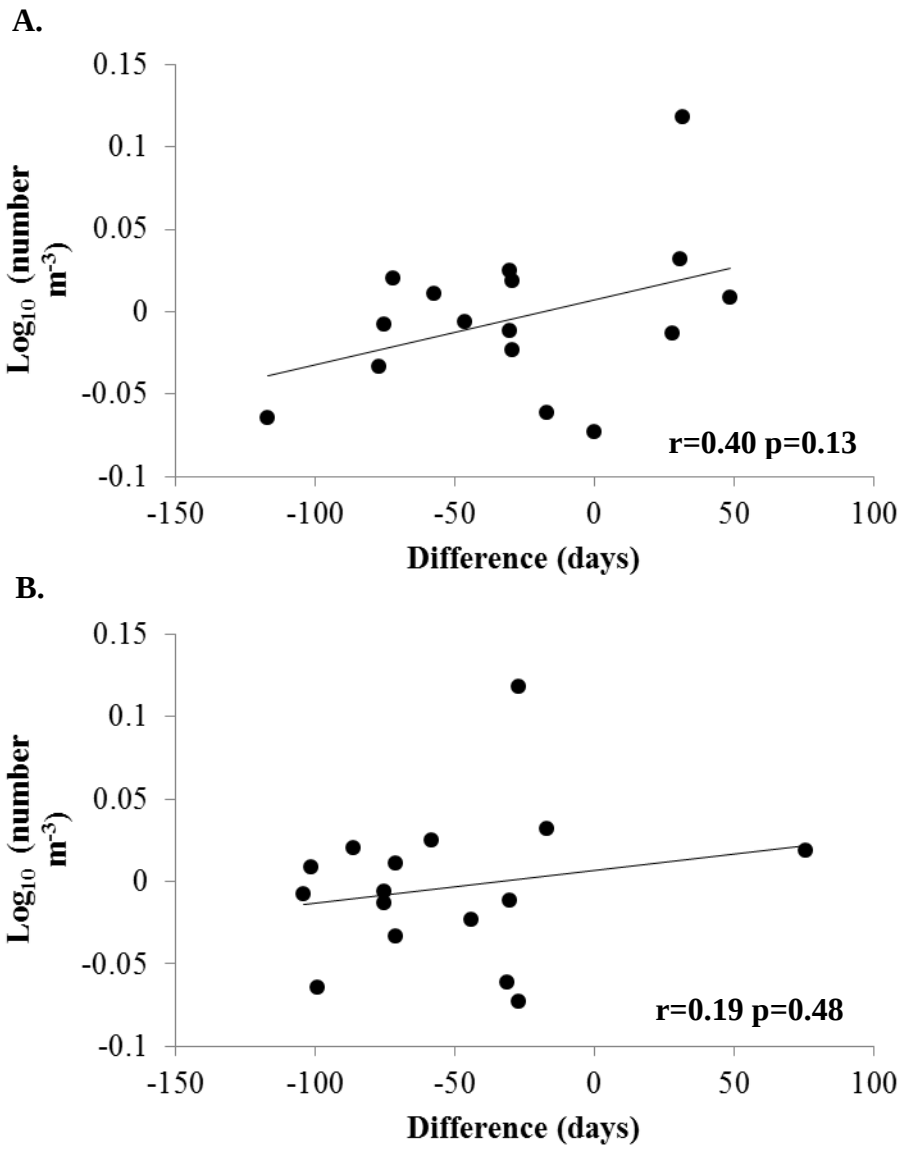

Figure 1.7 Difference in date of maximum occurrence of *Anchoa mitchilli* and arrival date *A. tonsa* adults (A) and copepodids (B) against detrended yearly average *A. mitchilli* densities for data between March and September.

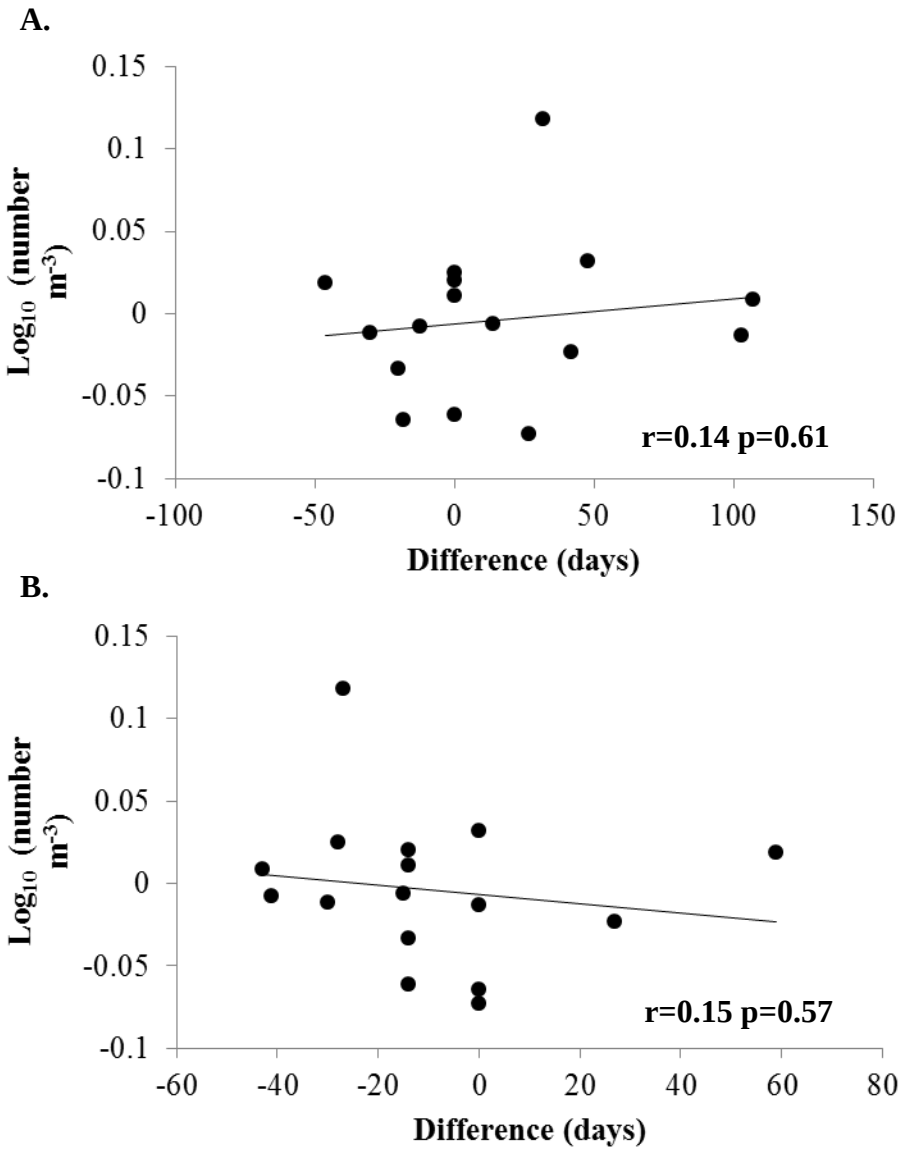

Figure 1.8 Difference in arrival date of *Anchoa mitchilli* and *A. tonsa* adults (A) and copepodids (B) against detrended yearly average *A. mitchilli* densities for data between March and September.

Chapter 2

Long-term decline in bay anchovy larvae (*Anchoa mitchilli*) in a Southeastern estuary; influence of freshwater discharge

2.1 Introduction

Coastal estuaries have been subject to increasing stressors over the past several decades due to coastal development, human population growth, and climate change (Kennish, 2002; Paerl et al., 2006). More specifically, freshwater delivery to coastal systems have been directly altered in recent years through increased human modification of hydrologic regimes and climate change (Flemer and Champ 2006; Wetz et al., 2011). In addition to freshwater, rivers also deliver nutrients which support productive and diverse coastal ecosystems (Whitall et al., 2003; Wetz et al., 2011). Drought or low flow conditions during recent years may be associated with lower biological productivity in coastal waters (Nixon and Buckley, 2002). Wetz et al. (2011) showed that decreases in freshwater input to the Neuse River Estuary, NC led to declines in nutrient levels and mesozooplankton abundances during a period of drought. These changes have the potential to influence upper-trophic level organisms through altering food supply (Wetz et al., 2011; Sheldon and Burd, 2014).

North Inlet, SC (NI) is one region reliant on nutrient delivery to support coastal production; work by Dame et al. (1986) showed that there was a net import of chlorophyll a (Chl-a) into the system from the adjacent coastal ocean meaning that concentrations of Chl-a within the estuary are dependent on coastal production. NI's

adjacent estuary, Winyah Bay (WB) delivers the majority of freshwater into the local, coastal waters. The entire watershed of WB is the third largest along the east coast of the US (Buzzelli et al., 2004). Nearly 25% of South Carolina's total land area and nearly 20% of North Carolina's total land area are included within the watershed. The main source (>85%) of fresh water input into the system is received through the Pee Dee-Yadkin river system (Patchineelum et al., 1999).

Coastal estuaries act as critical habitat for many fish species of primary ecosystem and economic importance (Boehlert and Mundy, 1986). Larvae of members from Sciaenidae, Clupeidae, and Engraulidae famalies can be found throughout intertidal creeks of NI (Allen and Barker, 1990). One species of the Engraulidae family, the bay anchovy (*Anchoa mitchilli*) is particularly abundant and represents a critical trophic link in estuarine food webs (Jonhson et al., 1990; Scharf et al., 2002). Ogburn et al. (1988) conducted a four year study which revealed *A. mitchilli* to be the most abundant fish species within NI during spring and summer, however scientific surveys indicated that their populations have declined over the past 30 years (Allen and Barker, 1990). Within NI, adults primarily feed on crab megalopae, crab zoea, veliger larvae, and calanoid copepod species (adults and copepodids) (Johnson et al., 1990). *Acartia tonsa*, a documented prey item, is a calanoid species whose production may be dependent on primary production (Durbin et al. 1983). The importance of *A. tonsa* in the diet of adult and larval bay anchovy has been well studied (Detwyler and Houde, 1970; Johnson et al., 1990; Peebles et al. 1996). Peebles et al. (1996) produced work suggesting that bay anchovy are income spawners (i.e., their fecundity is reliant on prey levels at and shortly before spawning) and that *A. tonsa* was their primary prey in the Tampa Bay system.

Improving scientific understanding of the environmental factors which influence the productivity of fish populations in coastal ecosystems is vital to their prudent management and utilization, especially as the potential influence of anthropogenic climate change grows in the future. Here, I intend to contribute to this understanding by considering how changes in river discharge can influence larval abundance, offering insight to how the ecosystem might respond as precipitation and flow patterns continue to vary. I first sought to answer how lower trophic levels as measured by copepod density and Chl-a concentration would respond to reduced river discharge. It was my primary goal to explore the extent to which copepod abundance contributed to the interannual variability in larval abundance in order to relate freshwater and larval anchovy abundance in NI. Yearly averages of river discharge and Chl-a concentrations were compared to address the relative contribution of changes in flow to changes in production. Similar comparisons were completed for Chl-a and copepod density and copepod density and *A. mitchilli* density. I hypothesized that during a period of low flow, primary production (as measured by Chl-a concentration) and populations of higher trophic-organisms would be reduced thus contributing to the long-term decline in *A. mitchilli* abundance. Because *A. tonsa* is a primary food source of *A. mitchilli* (Peebles et al., 1996), and *A. tonsa* production is reliant on primary production (Durbin et al., 1983), I suggest the following relationship; reduced Chl-a concentrations resulted in lower copepod densities and therefore reduced egg production in *A. mitchilli* over an interannual time scale (**Fig. 2.1**). Lower than average copepod densities reduced survival and subsequent recruitment, diminished the number of one-year females, and contributed to lower larval abundance in subsequent years. I utilized a suite of long-term datasets

including *A. tonsa* and larval *A. mitchilli* densities, Chl-a concentrations, discharge rates, and surface salinity to address the aforementioned hypotheses.

2.2 Methods

2.2.1 Study Area

Time series data were collected in NI. The estuary is a *Spartina alterniflora* dominated salt marsh and is protected through the National Estuarine Research Reserve System (NERRS). It is a well-mixed system with mean salinities ranges from 30-35 ppt. Zooplankton collections were made at one site (BB) in Town Creek; a subtidal channel which has a typical depth between 2.5-4 m at low tide (Allen and Barker, 1990). The sampling site (BB) is located at the confluence of two creeks, Town and Clambank (CB). The site has been described in detail by Allen et al. (2008), and Buzzelli et al. (2004). Chl-a data were measured from samples collected at the NERR long-term sampling site (Oyster Landing-OL) within Crab Haul Creek (33°20'58" N, 79°11'34" W) (**Fig. 1.1**). The site has been described in detail by Buzzelli et al. (2004). For full description of study area refer to Chapter 1.

2.2.2 Biological Sampling

Multiple time series were utilized, including measurements of mesozooplankton, larval bay anchovy density, and Chl-a concentrations. For complete description of methods used in the collection of larval fish and mesozooplankton, refer to Chapter 1. Collections for Chl-a analysis were made daily beginning April of 1983 at OL and data were available for the years of 1983-2002. Data available from Clam Bank were temporally limited (i.e., only available for the years 1983-1993) and monthly averages for this period were correlated to the monthly averages at OL ($r=0.91$ $p<0.01$) (**Fig. 2.2**).

Individual values represent the measured Chl-a concentrations the day prior to the biweekly mesozooplankton sampling. A 1-L surface water sample was collected at approximately 1000 hours EST. Between 10 to 20-mL of this water sample were filtered through a 2.5-cm, 0.7-µm (nominal pore size) GFF. The filter was placed into a scintillation vial with 1 mL of saturated magnesium carbonate ($MgCO_3$). After freezing, samples were removed and 9 mL of 100% acetone was added, and then refrigerated for 24 hours. After 24 hours, the samples were removed, shaken, and returned to the fridge for an additional 24 hours. After extraction was complete, a Turner Model 101 Fluorometer samples to analyze collected between 1983 and 1994. A new Sequoia-Turner Model 450 Digital fluorometer was used with a NB440 nanometer filter beginning with the January 8, 1994 sample event. Use of a 430-nm filter makes Chl-a and phaeophytin indistinguishable thus, for the samples collected between 1983 and 1993, hydrochloric acid was added to obtain a phaeophytin a value which was then subtracted from the total to give a Chl-a value. These steps were not necessary for samples collected after January 8, 1994 as the NB440 filter used in analysis is specific to Chl-a.

2.2.3 Pee Dee River Discharge

For analysis including river discharge data, I used mean monthly and yearly discharge data recorded at U.S. Geological Survey (USGS) station 02131000 located on the Pee Dee River in Pee Dee, SC. The inclusive Pee Dee-Yadkin river system accounts for greater than 85% of freshwater input into the watershed, with the Pee Dee being the largest contributor (>60%) (Patchineelum et al., 1999). Due to its large percentage of input into NI-WB relative to other river systems, I chose to focus our analysis on data only taken from this site.

2.2.4 Data Analysis

The densities (number of individuals m^{-3}) of *A. tonsa* adults and copepodids and *A. mitchilli* larvae were calculated for each sample. These abundance values and individual Chl-a concentrations were used to calculate monthly and yearly averages. Yearly averages were used to make comparisons over an interannual time scale. Only sampling dates between the months of March and September were included in yearly averages due to the seasonal occurrence of *A. mitchilli* (April-September). Monthly averages were utilized in order to address the contribution to variability during peak spawning period. The main focus of monthly comparisons was June averages which represents the average date of maximum occurrence for larval bay anchovy (**See Chp. 1**). Monthly data were detrended prior to correlation analyses to remove similar long-term trends by fitting a line over the given time period and model values were produced from the fitted line. These model values were subtracted from the original values to achieve detrended values. Long-term trends and correlations were determined using linear regression and Pearson two-tailed correlation tests respectively.

2.3 Results

2.3.1 Long-term Trends

A significant negative trend ($p<0.01$) was noted in monthly average concentrations of Chl-a, monthly average densities of *A. tonsa* adults and copepodids, and monthly average densities of *A mitchilli* larvae from 1981-2002. *A. tonsa* adults maximum density was recorded on 06/29/1981 (24561 individuals m^{-3}) and copepodids maximum density was recorded on the same date and measured approximately 48616 individuals m^{-3}. The overall average density of adults and copepodids was approximately

1317 and 3670 individuals/L respectively. The maximum number of *A. mitchilli* larvae was recoded 4/30/1981 (10 individuals m^{-3}). Chl-a concentrations reached their maximum value 07/09/1991 (29.53 µg/L). Time series reveal similar seasonal cycles for each group; peaks in late spring and summer each year (**Fig. 2.3**).

Significant negative trends ($p<0.05$) were also noted in monthly average concentrations of Chl-a and copepodid densities in the months of April, May and June between the years of 1981 and 2003 (**Fig. 2.4**). Yearly averages (March-September) also revealed significant negative trends ($p<0.05$) for Chl-a concentrations and copepodid and adult densities (**Fig. 2.5A**). Detrended yearly averages of Chl-a concentrations were correlated to detrended adult densities ($r=0.81$ $p<0.01$) (**Fig. 2.5B**) and copepodid densities ($r=0.72$ $p<0.01$) (**Fig. 2.5C**) between the years of 1983-2002. Additionally, a long-term decline was noted for yearly average anchovy densities ($r=-0.79$, $p<0.05$) (**Fig. 2.6**).

2.3.2 Relationship Between Copepods and Larval Density

It was my primary goal to assess the relative contribution of *A. tonsa* densities to the interannual variability in larval abundance. Monthly and yearly detrended densities of *A. tonsa* copepodids and adults and larval bay anchovies were compared but I found there was no significant relationship between copepods and anchovies on an interannual timescale. Given that *A. mitchilli* are considered income spawners, I was motivated to compare densities of copepods and fish larvae during the fish's peak spawning period (i.e., June) (See **Chp. 1**). Thus, I compared densities of *A. tonsa* and larval during the month of June. I found no statistical relationship between the densities of larval *A. mitchilli* and copepods when comparing detrended time series (**Fig.**

2.7A). However, a significant relationship was present between the two time series prior to removing the trend ($r=0.715$, $p<0.05$)(**Fig 2.7B**). It is important to note that the statistical significance of this relationship is reliant on the shared long-term trend between the two groups. All other individual months were compared and revealed no significant relationship (data not shown). I tested the interannual relationship between larval anchovy and *A. tonsa* densities through comparing yearly averages which included data from between the months of March and September, there was no significant relationship present (**Fig. 2.8**)

Throughout the time series, *A. tonsa* comprised nearly 35% on average of total copepods. Other copepods may be suitable prey and could supplement the diets of both adult and larval bay anchovy. Therefore, I also investigated the relative contribution of total copepods to the interannual variability in larval abundance. Similar to *A. tonsa*, there was no significant relationship between total copepods larval abundance for yearly June averages or yearly averages unless time series are not detrended ($r=0.78$ $p<.05$) (**Fig. 2.9**).

2.3.3 River Discharge

River discharge measured at U.S. Geological Survey (USGS) station 02131000 (Pee Dee River) varied greatly between 1981 and 2002 (**Fig. 2.10A**). Between the years of 1983 and 2003 a significant decline in discharge was noted ($r= -0.472$, $p<0.05$). Mean yearly discharge between 1981 and 2003 was approximately 2666.7 m^3/s with a standard deviation of nearly 1025.4 m^3/s. Yearly average discharge between the months of March to September were significantly correlated with average salinities within NI for the same period ($r= -0.801$, $p<0.05$) (**Fig. 2.10B**). Yearly average discharge

was also compared to Chl-a concentrations, copepod densities, and *A. mitchilli* densities. Of all the groupings, a significant relationship was present only between *A. mitchilli* larval density and river discharge ($r=-0.447$, $p<0.05$) (**Fig 2. 11**).

2.4 Discussion

I attempted to assess the relative influence that interannual variability in freshwater discharge could have on *A. mitchilli* larval abundance. By comparing a suite of long-term data sets, I noted a significant negative trend ($p<0.01$) in monthly average concentrations of Chl-a, monthly average densities of *A. tonsa* adults and copepodids, and monthly average densities of *Anchoa mitchilli* larvae from 1981-2002. I hypothesized that the interannual variability in *A. mitchilli* could be attributed to changes in their food supply (i.e., *A. tonsa*) which would be a response to variability in river discharge.

The idea that prey availability may have a significant influence on larval fish survival and eventual recruitment is not novel. The factors contributing to interannual variability in larval recruitment have perplexed scientists for over a century (Hjort, 1914). Various hypotheses have been proposed to explain why there is such great variability between sequential recruitment classes (Houde, 2008), and a focus has been placed on the availability of prey (Lasker, 1985; Cushing, 1990). However, drawing quantitative relationships between recruitment and prey abundance has proven to be difficult (Cushing, 1995). In my own results, no relationship between *A. mitchilli* larval abundance and *A. tonsa* density was noted at interannual scales, which may be due to multiple possibilities. In Tampa Bay, Florida *A. mitchilli* egg production was correlated to *A. tonsa* abundance leading the authors to suggest that the fish is an income spawner

with a spawning rate sensitive to the availability of *A. tonsa* (Peebles et al., 1996). Within NI, it is possible that *A. tonsa* is not a substantial food source for adult and larval anchovy. Johnson et al. (1990) conducted a study to characterize prey selection by adult bay anchovy relative to prey availability within NI. Their study found that although *A. tonsa* comprised nearly 47% of the total zooplankton collected, *A. tonsa* only accounted for approximately 7% of the adult diet. In the samples used for this study, *A. tonsa* comprised approximately 35% of total copepod density on average. The lack of significant relationship between *A. tonsa* and anchovy larvae and the lower percentage which *A. tonsa* comprises of total copepods, could suggest an alternative food source. To address the possibility of an alternative food source I tested the interannual relationship between total copepods and *A. mitchilli* abundance. Yet, similar results were produced. This may suggest that copepods may not be the most substantial food source in terms of promoting egg production in adults and/or larval survival on an interannual scale or that starvation is not a major source of mortality.

In another system, Chesapeake Bay, a similar decline has been seen in *A. tonsa* and *A. mitchilli* abundance (Kimmel et al., 2012). These authors attribute the long-term decline in *A. tonsa* to increased eutrophication and a subsequent increase in the predator *Mnemiopsis leidyi*. A decline in *A. mitchilli* was attributed to the availability of *A. tonsa*. However, Kimmel et al. (2012) attributes the decline in *A. mitchilli* to a decrease in its prey *A. tonsa* yet, offered no statistical evidence of the interannual relationship between anchovy and *A. tonsa*. Additionally, they neglect the fact that *M. leidyi* also exerts pressure on *A. mitchilli* through predation on their eggs (Monteleone and Duguay, 1988). This is most likely due to the fact that the data on *M. leidyi*

population is limited within Chesapeake Bay (Kimmel et al., 2012). A significant relationship between Chl-a and *A. tonsa* densities within NI may reveal an influence of prey availability on production within the system. The two regions (i.e., NI and Chesapeake Bay) differ substantially. Most notably, NI has not seen an increase in eutrophication events in recent years, and there has been no reported increase in *M. leidyi* or other predators of *A. tonsa* and *A. mitchilli*. Additionally, NI is under limited direct human influence. With greater than 95% of the surrounding land area still in its natural state and limited fishing within the estuary, NI could be seen as a representation of a pristine, model coastal estuary.

Within NI, I attribute the decline in *A. tonsa* to be bottom up controlled and suggest the reduction in Chl-a concentrations over the 20 year period has led to decreased copepod production (**Fig. 2.5**). Originally, I anticipated that these declines in Chl-a concentrations and *A. tonsa* densities may be associated with changes in *A. mitchilli* populations. Peebles et al. (1996) showed that egg production by *A. mitchilli* and *A. tonsa* abundance were correlated within the Tampa Bay system suggesting they are income spawners (i.e., fecundity is dependent on prey availability). In reference to my hypothesized conceptual model (**Fig. 2.1**), if we assume that egg production by bay anchovy is dependent on the density of *A. tonsa*, then we expect anchovy which spawn in prey rich waters to produce more eggs and the larvae which hatch from these eggs to be less likely to starve during the critical period. This would result in a positive correlation between *A. tonsa* and larval bay anchovy abundance; something not reflected by the current data. Because most of the egg production comes from year-one females (Peebles et al., 1996), subsequent poor year classes could contribute to this long-term decline.

Although our results produce no concrete evidence linking copepod and anchovy larval abundance, there are multiple possibilities to explain this lack of relationship. One possibility is that using *A. tonsa* and total copepods abundance as a representative of lower trophic level and primary food source of bay anchovy may not be ideal given the lack of significant relationships. Future studies may benefit from characterizing the mesozooplankton catch more specifically as well as characterizing what prey is contained within adult and larval anchovy guts throughout the spawning season. Additionally, egg production and larval abundance are not always related due to spatial patchiness and high mortality between the life stages (Houde and Lovdal, 1985; McGurk, 1986). This could lead to spatial mismatch between predator and prey and possibly introduce larvae to conditions of low prey density despite high levels in other regions.

Winyah Bay supplies a significant amount of freshwater and the accompanying nutrients to the adjacent coastal region. Dame et al. (1986) showed that there is a net import of Chl-a into North Inlet from the coastal region. A decline in freshwater discharge may have led to reduction in nutrient delivery to the adjacent coastal waters (Whitall et al., 2003; Wetz et al., 2011). This reduction would support less productive waters which can be seen in the long term declines of Chl-a, *A. tonsa*, and *A. mitchilli* (**Fig. 2.2**). Here I provided evidence of long-term change within an estuary under low human influence. However, no relationships could be established on the interannual scale between larval anchovy and copepod densities. Additionally, an inverse relationship between river discharge and anchovy density was present (**Fig. 2.11**). Thus, my original hypothesis is rejected. The presence of a negative relationship may suggest that there may be a larger scale process influencing both or that variability in discharge

may be contributed to the processes which control reproductive success of *A. mitchilli*. As the potential of future climate change to alter global and regional river flow patterns grows, it is vital to further explore possible biological impacts in our coastal estuaries.

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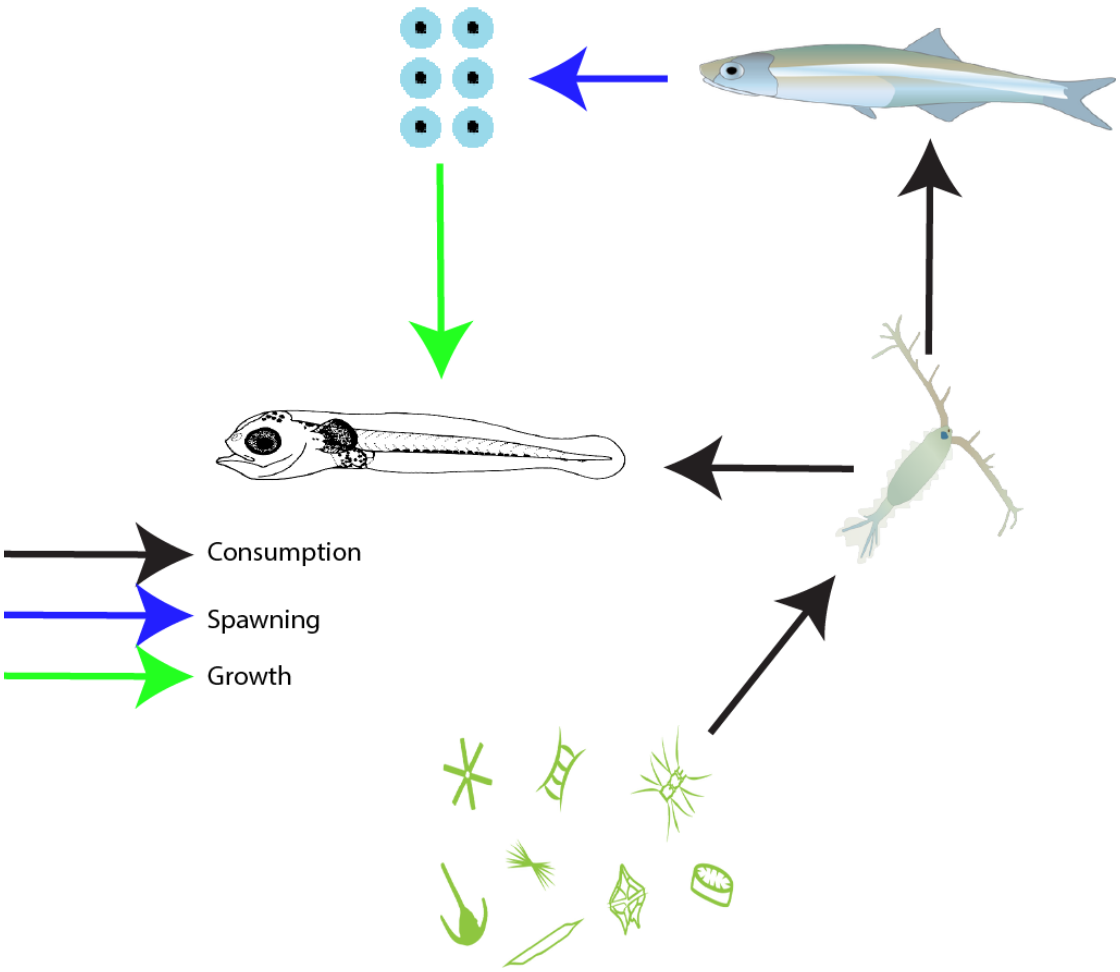


Figure 2.1 Suggested relationship between phytoplankton, *A. tonsa*, and *A. mitchilli*. within Winyah Bay System. The abundance of copepods directly influences spawning intensity and larval survival in other systems.

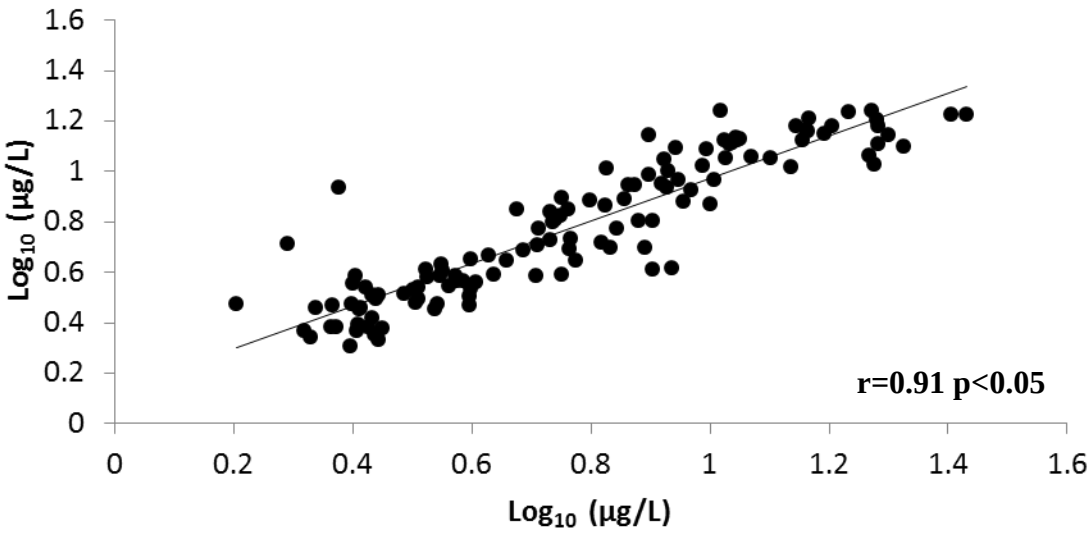


Figure 2.2 Relationship between monthly Chl-a average concentrations at OL(X-axis) and CB(Y-axis) between the years of 1983 and 1993.

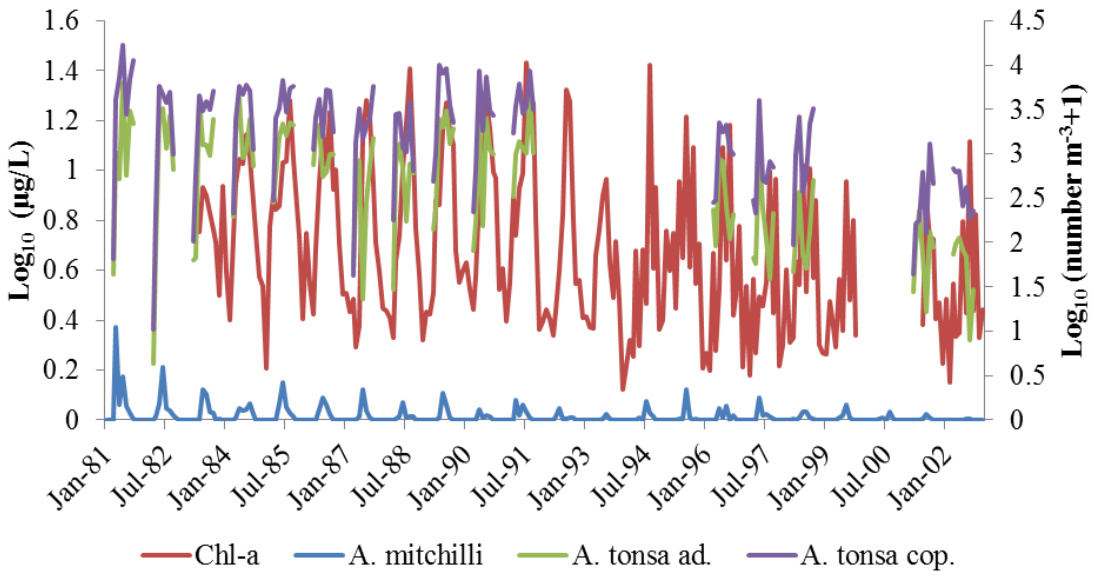


Figure 2.3 Average monthly (March-September) concentrations of Chl-a (µg/L) and densities of *A. tonsa* copepodids (cop), *A. tonsa* adults (ad.), and *A. mitchilli.* larvae (number m^{-3}) from 1981-2002.

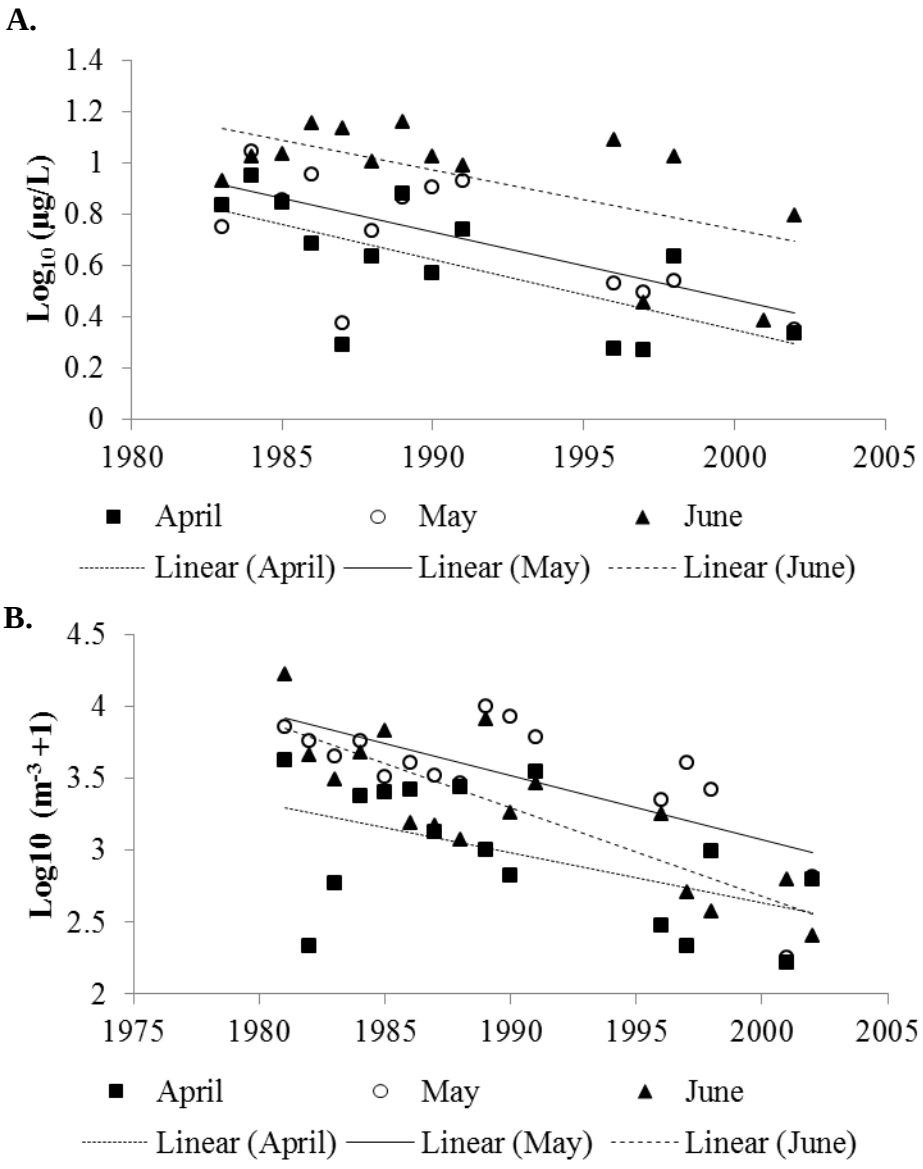


Figure 2.4 Average monthly concentrations of Chl-a from 1983-2003 for the months of April, May, and June.**(A)** Average monthly densities of *A. tonsa* copepodids from 1981-1991, 1996-1998, and 2001-2002 for the months of April, May, and June.**(B)**

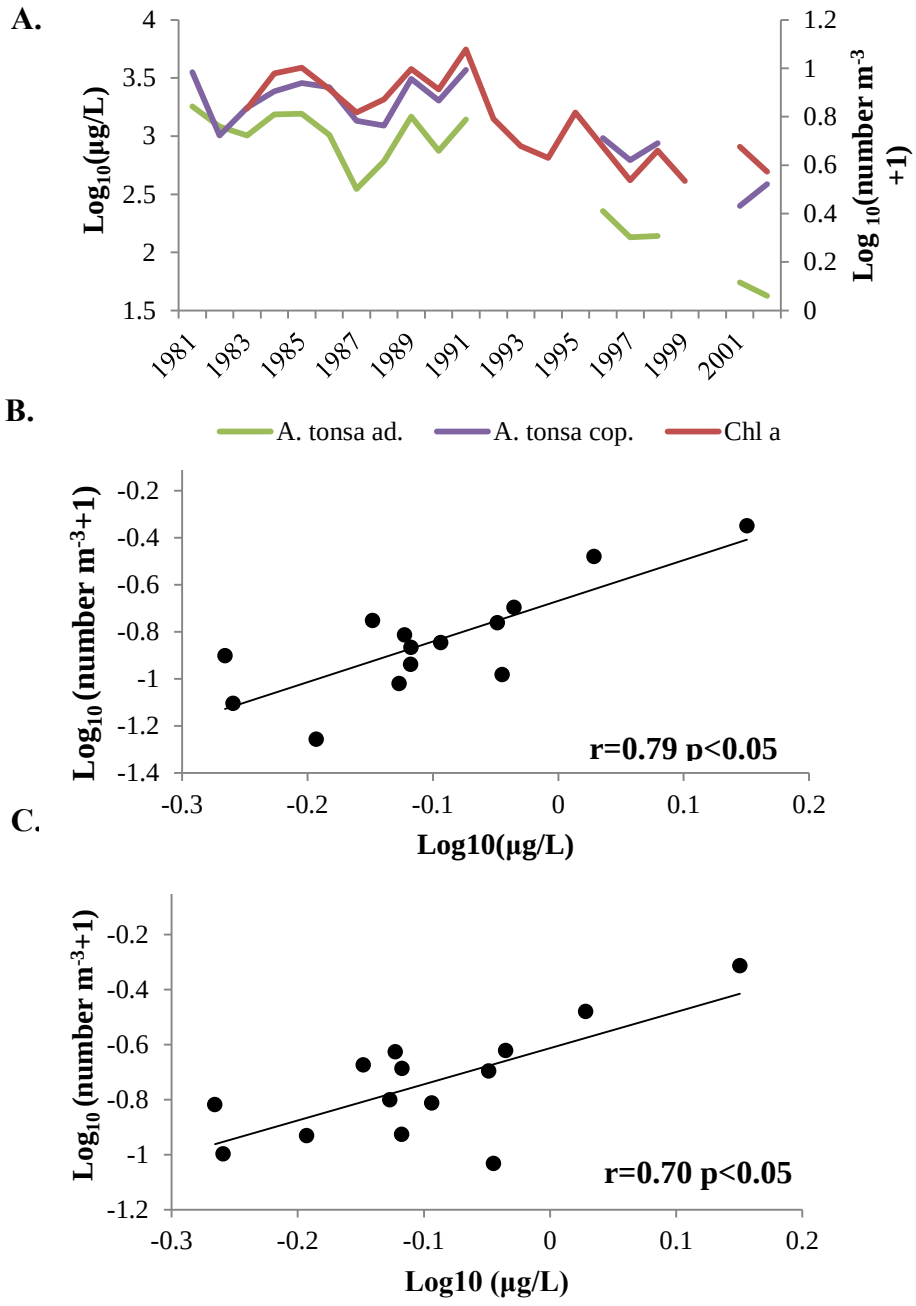


Figure 2.5 Time series of yearly averages (March-September) for Chl-a , *A. tonsa* adults ,and *A. tonsa* copepodids **(A).** The relationship between detrended yearly averages of Chl-a concentrations and A. tonsa Adults **(B)** and copepodids **(C)** densities from 1983-1991, 1996-1998, and 2001-2002.

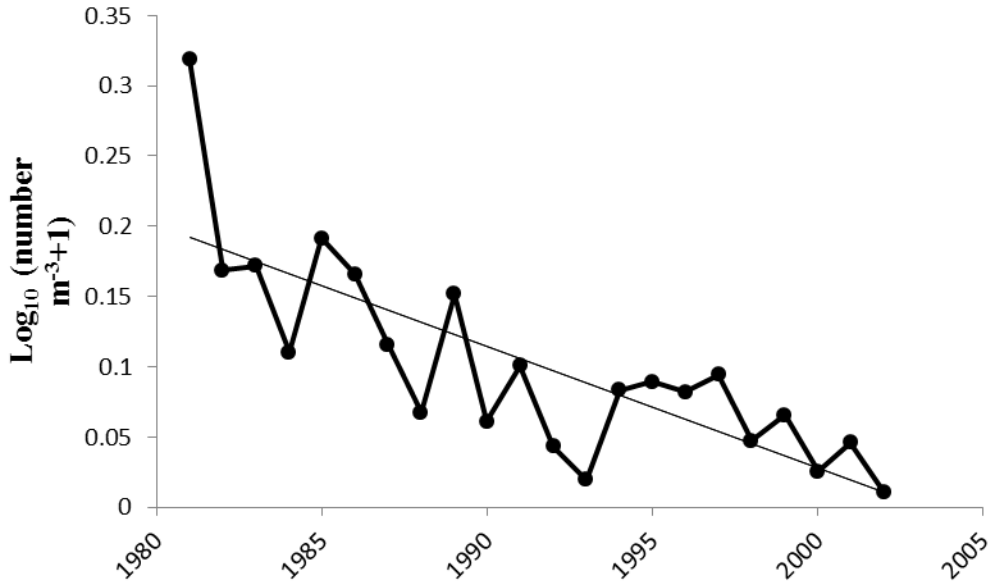


Figure 2.6 Yearly average *A. mitchilli* larval densities for the months of April and May from 1981-2002.

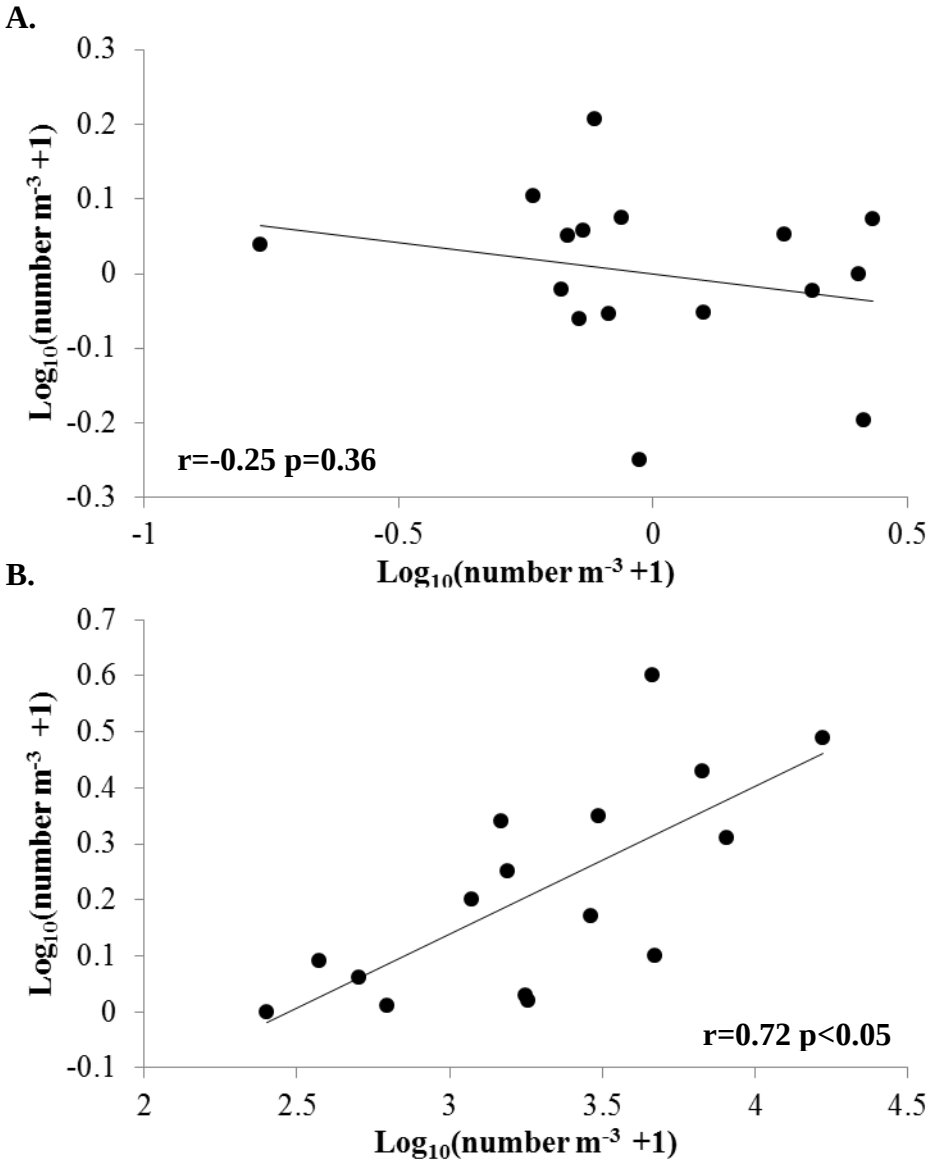


Figure 2.7 Detrended yearly averages of *A. mitchilli* (y-axis) larvae for the month of June and *A. tonsa* copepodids (x-axis) (**A**). Yearly average densities of *A. tonsa* copepodids (x-axis) and *A. mitchilli* larvae (y-axis) for the month of June (**B**).

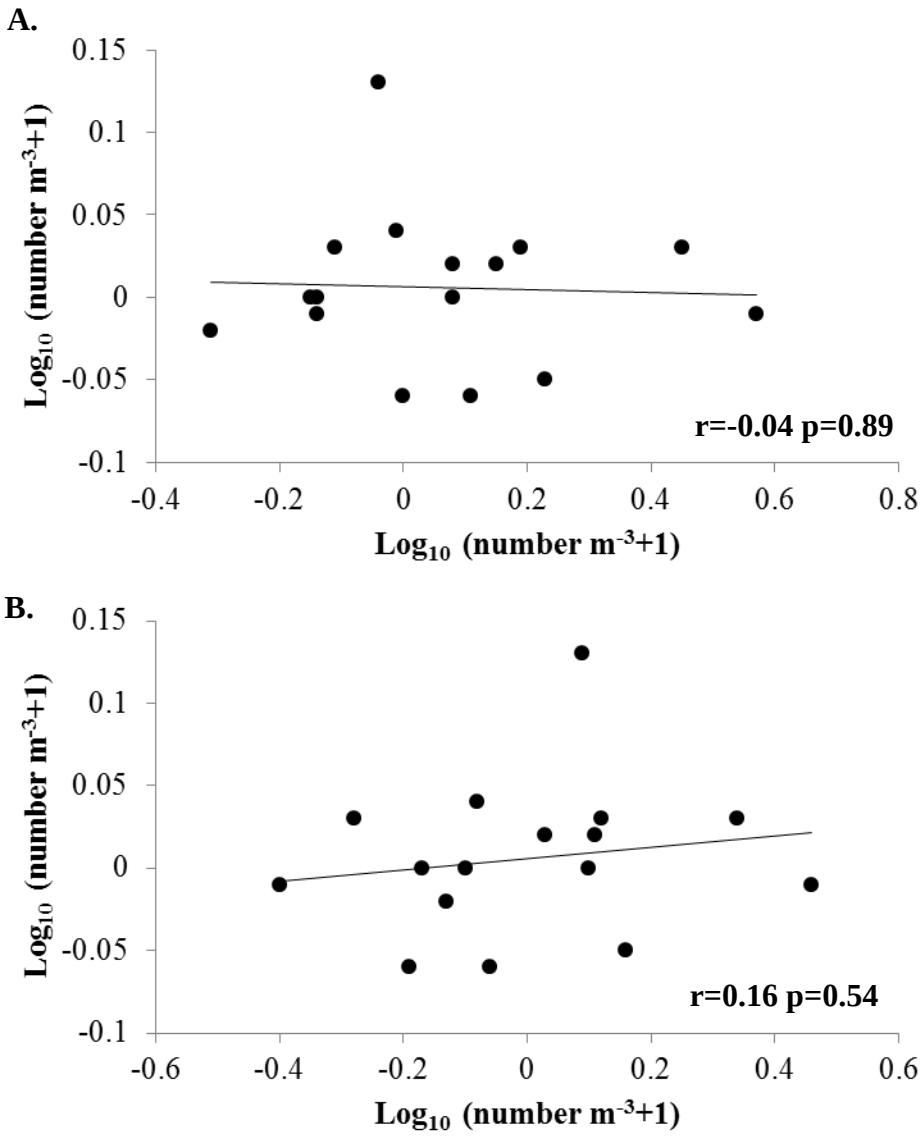


Figure 2.8 Detrended **y**early averages of *A. mitchilli* (y-axis) and *A. tonsa* adults (**A**) and copepodids (**B**) (x-axis).

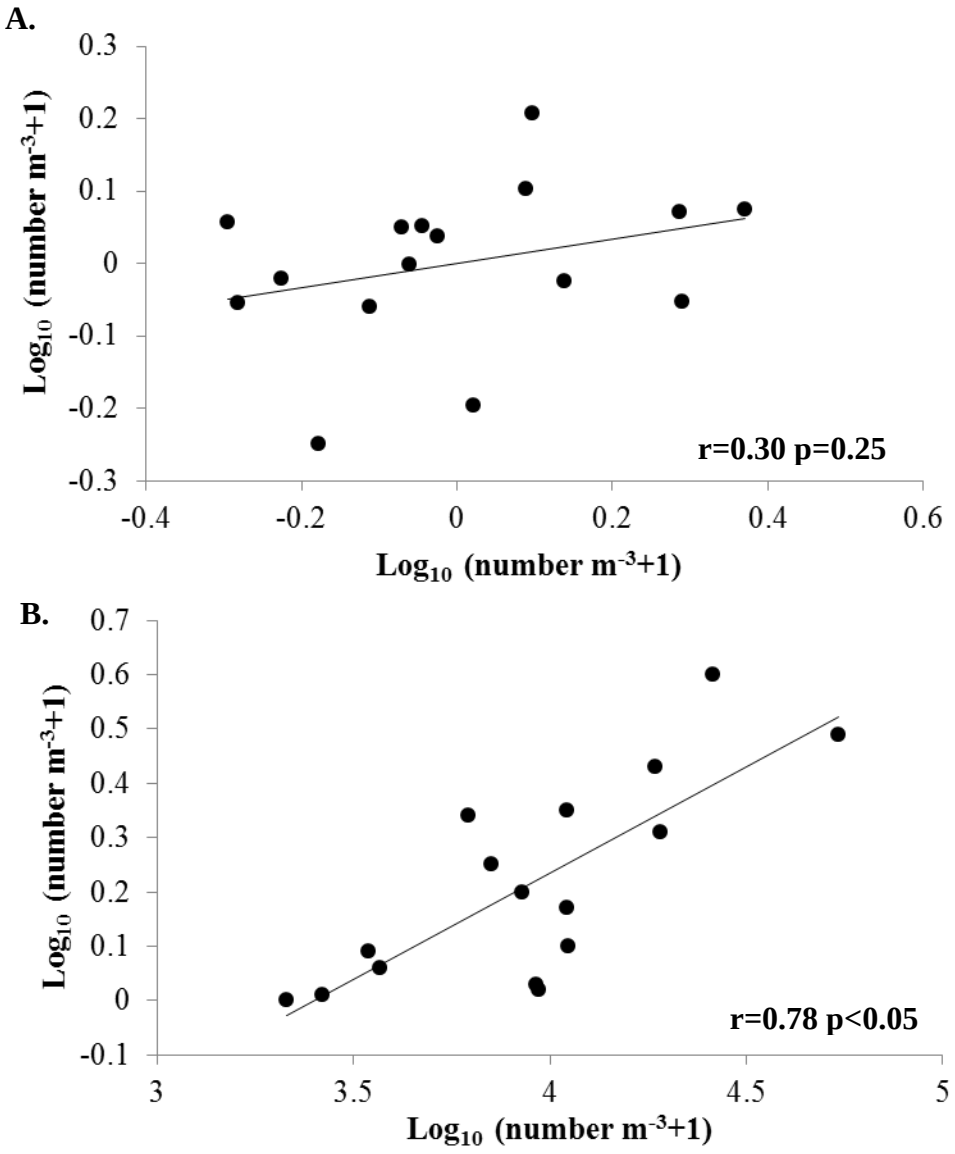
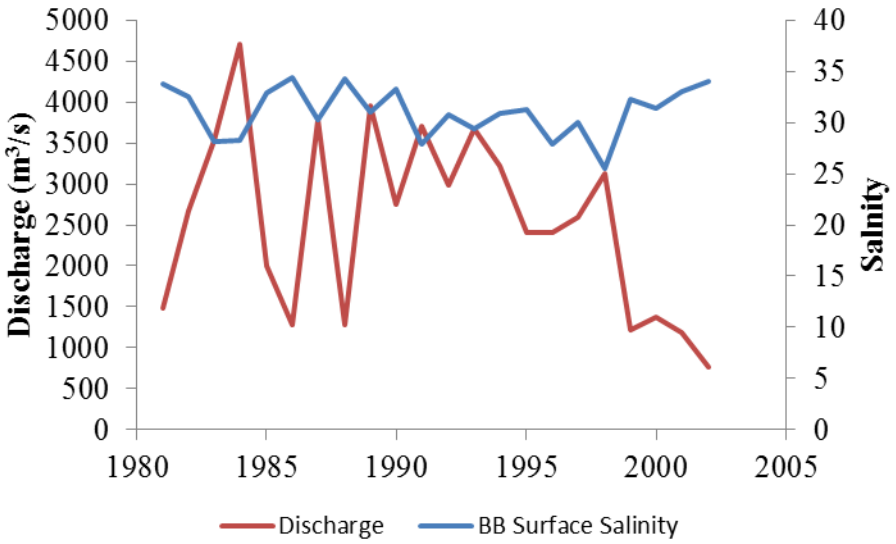


Figure 2.9 Detrended **y**early averages of *A. mitchilli* (y-axis) and total copepods for the month of June (x-axis) (**A**). Yearly averages of *A. mitchilli* larvae (y-axis) and total copepods for the month of June (x-axis)(**B**)

A.



B.

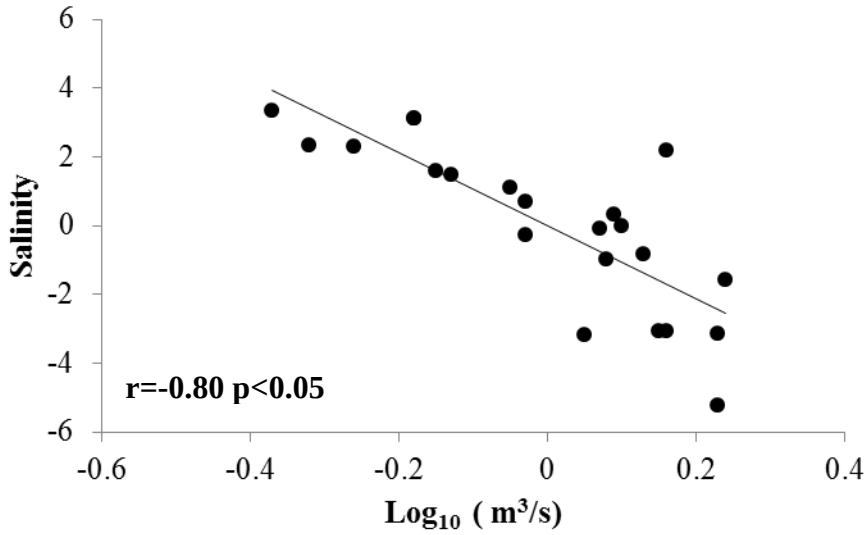


Figure 2.10 Time series of river discharge and salinity between 1983 and 2003 (**A**). Detrended yearly average (March-September) Pee Dee River discharge and surface salinity within North Inlet (**B**).

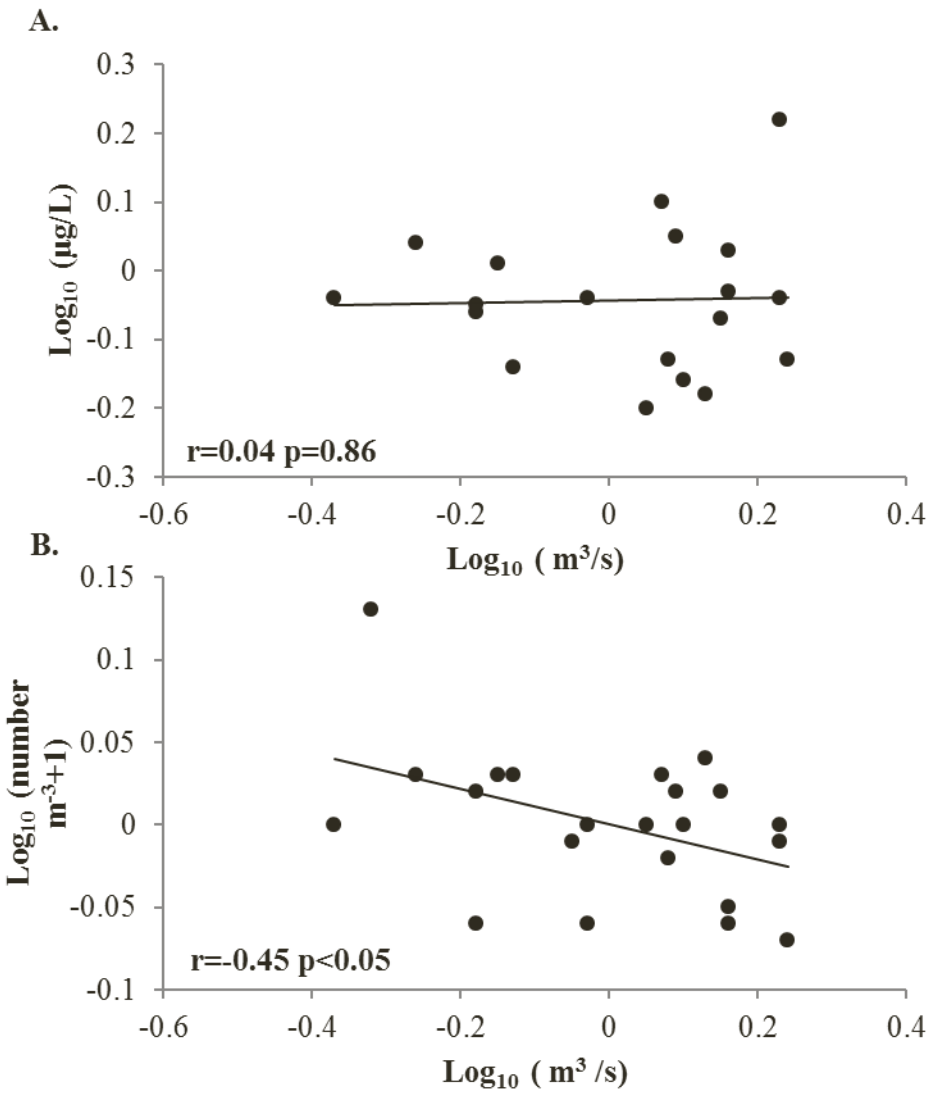


Figure 2.11 Detrended yearly averages of Pee Dee river discharge and Chl-a concentrations (**A**) and larval anchovy densities (**B**).